

XI.—*An Introduction to the Study of the Drepanididæ, a Family of Birds peculiar to the Hawaiian Islands.* By ROBERT C. L. PERKINS, B.A.\*

REMARKABLE as are some other members of the Hawaiian Avifauna, yet it is upon the Drepanine birds that the interest of the ornithologist will always be centred. The Drepanididæ, as here considered, include thirty-six species, belonging to no less than eighteen genera. One genus with one species is restricted to the outlying island of Laysan, as is also a second species not generically peculiar, both being included in these remarks on the family, although with the rest of the Laysan Avifauna they may be excluded from the list of Hawaiian forms. The total number of species here cited is rather less than that given by the latest writers on the Archipelago, owing to the fact that several forms which have been described as distinct appear to be quite unworthy of such rank.

1. *Small proportion of Species as compared with Genera.*

If we compare the Drepanine birds with the peculiarly Hawaiian families in other groups of animals, we are at once struck by the very large number of genera accepted as compared with species. No doubt this is partly due to the very different value attached to characters supposed to be generic by systematic workers in different lines, and also to the large size of birds as compared with many other creatures, owing to which their characters are obvious on the most casual inspection. If we compare the Drepanididæ with such a family as the Proterhinidæ in the Beetles, which is also peculiar to the Hawaiian Islands, we do not find the latter susceptible of easy division into well-marked genera as in the birds; indeed, at present the members are all included in a single genus. Yet to the student of both groups it is obvious that the extreme forms of the Proterhinidæ exhibit differences of structure as great and varied as are found in the extreme forms of the Drepanididæ; in fact the variety of

\* Communicated by the Joint Committee appointed by the Royal Society and the British Association for investigating the Zoology of the Sandwich Islands.

structure is probably greater in the beetles. If, however, we were to reduce the hundred and thirty species of *Proterhinus* to the number of species of the Drepanine birds, and particularly if in doing so we were to eliminate the osculant forms, it is manifest that the condition of the two groups would be strikingly analogous. It is therefore in my opinion clear that, making all allowance for the ease with which the one group is studied, and the relatively great difficulty presented by the other, there is a real and great difference between the Drepanididæ and the Proterhinidæ, and in fact between these birds and most of the other extensive and peculiarly Hawaiian groups of animals, and that the difference is due to the fact that while in the birds there has been a keen competition for existence between the various species and between the individuals of each species, in the Proterhinidæ there has been little or none, because the food-supply of the latter, consisting of dead wood, is in a forest-covered country almost unlimited. As will be hereafter noticed, there is good reason to believe that the competition between the birds has been much more keen in past times than during the more recent periods of their existence.

## 2. *Origin of the Drepanididæ doubtful.*

If we compare the Drepanididæ with other families of birds, it is obvious that, considering the few species that exist, they exhibit an unusual diversity of structure. As a proof of this, it is only necessary to mention the fact that competent ornithologists have repeatedly assigned to different families even those forms which *without any possible doubt* belong to the same. This diversity of structure must have required a vast time for its evolution, and the period at which the ancestral Drepanid immigrated to the islands must have been very remote indeed. Whether all the presently existing species of this group have been evolved from one original immigrant or from more we cannot say; but the former view is probably the more correct, although two ancestral immigrants might be admitted.

That the islands were originally stocked by *numerous*

species which produced the present family is highly improbable, seeing that whole families of birds far better adapted to cross wide extents of ocean are quite unrepresented in the Hawaiian Islands, although we know that some of them thrive exceedingly when imported, and many others would no doubt do so under similar circumstances.

Whence the ancestors of the present Drepanine birds came is, owing to their dubious relationships with outside forms, still an open question; though if it were certain that their closest relationship was, as Dr. Gadow has suggested, with the Cœrebidæ, little doubt would remain as to their American origin. For the present it is safer to consider them, with other peculiarly Hawaiian groups, as being of unknown origin.

3. *Two Groups of Hawaiian Drepanine birds exist, indicating either two distinct original immigrants or, more probably, very early divergence from one ancestor in two directions.*

I have already stated that a dual origin for the present Drepanines is conceivable, and is indicated by the fact that they fall clearly into two groups. The first of these contains six genera, viz. *Drepanis*, *Drepanorhamphus*, *Vestiaria*, *Himatione*, *Palmeria*, and *Ciridops*; the second the remaining twelve.

The genera of the first group are characterized by the truncate apices of the primaries, except in the anomalous *Palmeria*, and by the plumage of the young, which is always partly black or of a dull colour. In the adults white markings are present either on the wings or on the upper parts of the body. The skin, moreover, is comparatively thick, and sometimes extremely tough and thick, as cannot fail to be noticed by the collector when using very small charges of powder and shot to procure specimens. The plumage of the sexes is identical or nearly so. Red colours are acquired by the adults of some species in both sections, but in a totally different manner; in the second group it is invariably through a green or olivaceous stage, while green-plumaged forms are never found in the young of the first group. In addition it may be noted that the songs and cries of the members of the

first section are of a very different character from those of the second, between most of which there is a striking general resemblance in this particular. Further, all the members of the former which are known to me in life (*Himatione*, *Vestiaria*, *Palmeria*, and *Drepanorhamphus*) have a peculiar noisy flight, so that the sound caused by their wings, when they fly freely, can be heard at a long distance.

In the second group the primaries are never truncate at the apex; the young, moreover, are invariably clothed to a large extent in green or olivaceous plumage; and this colour nearly always persists in the adult female, although it may be totally lost in the adult male. Such is the case in several species of *Loxops*, the green coloration in this genus being largely permanent in the male of the Kauaian species only (*L. cæruleirostris*). There are almost always well-marked distinctions of colour between the adults of either sex. In a few forms which retain in the adult male and female the green plumage characteristic of immature birds (e. g., *Viridonia* and *Chloridops*) there is little or no difference in the colour of the sexes; but very rarely is this the case when the adults acquire a special coloration, as in *Loxioides*, in which the head is yellow, though somewhat less brightly coloured in the female.

To those who believe in the great significance of the very different character of the coloration of the young birds in these two groups (whatever change may take place in the adults), as well as of the development of striking sexual characters throughout nearly the whole of one of them, the necessity of distinguishing clearly between them will be apparent.

#### 4. *Development of Species in each Group along similar lines, and the reason for the same.*

When we examine, side by side, a full series of the forms it is obvious at a glance that each group has developed along similar lines. *Himatione* and *Palmeria* of the first are in general structure very like *Chlorodrepanis* and *Viridonia* of the second; *Drepanis* and *Drepanorhamphus* resemble *Hemignathus*; *Ciridops* may be compared with *Loxops*.

With *Ciridops* in one direction the evolution of forms in the first group ceases, while from *Heterorhynchus* the second proceeds through *Pseudonestor* to a series of thick-billed birds quite unrepresented in the first. Consequently in discussing these remarkably analogous forms the six thick-billed genera will here be excluded. Turning to the habits of the birds of the remaining twelve genera, eleven of these certainly and all probably (the habits of *Ciridops* being little known) contain at least some species accustomed to feed on nectar\*. At the present time the main supply of this food is derived from the *Metrosideros*—the well-known “Ohia-lehua” of the natives, and the predominant tree in the forests of all the islands. Around the masses of red blossoms of these trees may be seen at the proper season an assemblage of various kinds of birds, the scarlet “Iwi” (*Vestiaria*) and the green or yellow “Akialoa” (*Hemignathus*)—both with long curved beaks,—the crimson “Apapane” (*Himatione*) with moderate straight bill, and the green “Amakihi” (*Chlorodrepanis*) with moderate curved bill. The observer wonders for what purpose such extraordinary developments can have taken place. On the same flowers are numerous bees peculiar to the islands, shortest of all short-tongued bees, with a tongue one millimetre long, yet as well able to feed on the nectar as the “Akialoa” with its tongue of two inches

\* Not that nectar is ever the *sole* food, though a most important source of nutriment—so important to the adults of some species that at certain seasons no individual shot contains any trace of insect food. Few Hawaiian insects frequent flowers, and such as do, viz. one or two beetles and the Hymenoptera, are seldom if ever found in these birds’ stomachs. Nectar is undoubtedly absolutely necessary to the existence of *Himatione*, *Chlorodrepanis*, *Vestiaria*, *Hemignathus*, and *Drepanis*, as they are constituted; small moths, caterpillars, and spiders—their other food—would certainly fail them at certain seasons. The honey-sucking Drepanids and the Moho can be kept alive on nectar and sugar-cane juice. When a species becomes purely insectivorous here, it shows extreme modification, e. g. *Pseudonestor* and some *Heterorhynchi*, so that it may obtain special insects inaccessible to other forms. In the introductory part of the ‘Fauna Hawaiiensis’ it will be necessary to give much space to comparisons between the birds, reptiles, molluses, and insects, and between the insects themselves, as well as to the Botany of the Islands.

or more. An examination of the *Metrosideros* tree will shew that it is a species not peculiar to the islands, although, as above remarked, it forms so large a part of the whole forest. In its specific characters it is in a remarkably unstable condition, exhibiting many striking variations, as though it were now in process of being differentiated into several species. Many of these variations are of constant occurrence and widely spread; some are deemed worthy even of specific rank.

These facts appear to me to point to a comparatively recent "immigration" of this tree, and I cannot suppose that it has existed on the islands for the period of time which would have been necessary to produce the exceptionally great variety of structure exhibited by the Drepanididæ. Turning to other sources whence the food-supply may have been derived at a period antecedent to the arrival and spread of the "Ohialehua," we find very different conditions. All\*, or practically all, the plants visited by these birds for food had bell-shaped or tubular blossoms, in which the nectar was more or less hard to reach. Of these tubular-flowered plants there are several predominant genera, some of which are themselves restricted to the islands, and belong to various families, comprising hosts of peculiar species. Most striking of all are the arborescent Lobeliaceæ, not closely related to forms found in other countries. The multiplicity of these peculiar plants, and their isolation from foreign forms, bears a striking resemblance to the state of affairs with regard to the Drepanine birds themselves, indicating likewise an extremely ancient occupation of the islands; and as the latter are the glory of the Hawaiian ornithologist, so are the former of the Hawaiian botanist. To these flowers Drepanids of both sections are still partial, and some particularly so, while the development of their extreme forms is not comprehensible without a knowledge of Botany. That there has been in the past severe

\* We exclude from consideration the *Eugenia*, a local species, the blooms of which are superficially like those of *Metrosideros* and are attractive to birds; it is known outside the islands, and was probably introduced by the early native settlers.

competition for food between the various species which have similar habits, and between the individuals of each, cannot be doubted. The number of birds that can exist in a given area is obviously only that which can be supported when the food-supply is at a minimum. At the present day, when the "Ohia" is in bloom over miles of country, the food-supply seems inexhaustible; but between the flowering periods it is limited, and often leads to a decided migration of the birds either from one district to another, or to different elevations in the same district, where, owing to the varying climate, the trees blossom at different seasons. Certainly the arrival of the "Ohia" must have been a powerful agent in the increase of individuals of honey-sucking species; and the competition for food must have been much more keen previously. One can hardly doubt that the primitive Drepanid was a honey-sucker, and that the now purely insectivorous, as well as the thick-billed frugivorous forms, were a later development, although the honey-suckers were no doubt at all times partly insectivorous, as they are at present. With the increase of the insect-fauna there would certainly be a tendency among the honey-sucking forms to become more largely, or even entirely, insectivorous, as in fact has been the case. The examination of a series of species of the Lobeliaceæ will show great differences in the length of their flowers; and while in some the nectar can be reached by the moderate tongue of *Chlorodrepanis*, in others it can only be procured by the extremely long-billed and long-tongued forms of Drepanids, and the long-tongued Meliphagine Moho, the latter also a peculiar and probably very ancient denizen of the islands.

A series of observations made on one of the most superb of the Lobeliaceæ showed that it could only be fertilized by these highly specialized birds. In this species the pollen is mature before the stigma is exerted, by which time the pollen has vanished. The latter cannot be wind-borne, because it is shed in a viscid mass on contact, and so is constantly deposited on the bird's forehead, from which it is difficult to remove it. With these considerations in view the cause of the development of the most remarkable forms in each group of birds

becomes manifest, and this cause has produced *Hemignathus* in the one, and *Drepanis* in the other, so like one another in general structure, while really but remotely allied. How easily the extraordinary lengthening of the bill, to which the resemblance is mainly due, may have taken place, side by side with the increasing length of the tubular flowers, is apparent from the fact that in some of the species there is even now individual variation in this respect. It should also be stated that in immature specimens the beak is much shorter, and that in the freshly-hatched young of *Chlorodrepanis* it is a short wide member, instead of having a slender curved form as in older birds. In the long-billed forms the mandibles are almost invariably shorter in the more "conservative" females, which in my second group retain in the adult the more primitive coloration of the young, though the males assume a totally different dress.

5. *Transition from a largely Vegetable Diet to purely Animal Food.*

Of the genera *Loxops*, *Oreomyza*, and *Heterorhynchus* the members are mainly insectivorous, but each comprises some species which at times feed on the nectar of flowers. In *Loxops* and *Heterorhynchus* the tubular character of the tongue is fully preserved, yet they very rarely feed from flowers, and some of the species perhaps never do so. Certainly that of the latter genus which is found on Hawaii is purely insectivorous, feeding, after the manner of a Woodpecker, on beetles and other insects; but the other three allied species are less adapted to such a life, and the Maui form has been known to me to visit blossoms as a very rare occurrence, while the partiality that the extinct species of Oahu had for banana flowers was often noticed. That these birds, even when purely insectivorous, still retain the characteristic Drepanid tongue, is clearly due to the fact that it remains a most efficient organ for obtaining insect food—in *Heterorhynchus* for extracting the wood-boring beetles of which it is so fond; and in *Loxops* for securing caterpillars which live in the terminal buds of some forest trees, not to



mention other purposes. In *Oreomyza*, on the other hand, the tongue is much degraded from its normal structure, while only two of the species, and those but on the rarest of occasions, have been seen to suck honey, and then only from the shallow "lehua" flowers. The genus is almost entirely insectivorous and feeds chiefly on exposed caterpillars, spiders, and moths.

#### 6. *The Thick-billed Species of the Second Group.*

There still remain to be considered the thick-billed species of the second division of the Drepanines which have no similar forms in the first.

There are seven such forms, distributed in no less than six genera, one of the latter (*Psittacirostra*), with its single unmodified species, ranging over the whole group of forest-bearing islands. One species of a peculiar genus (*Telespiza*) is restricted to the outlying island of Laysan; another, also forming a peculiar genus (*Pseudonestor*), is found only on the mountain of Haleakala in Maui; while three peculiar genera with four species are confined to the large island of Hawaii, namely, *Rhodacanthis* with two species and *Loxioides* and *Chloridops* each with one. It is now generally conceded that all these forms are only extreme modifications of the more normal Drepanines. In my published notes it is true that I placed this section under the Fringillidæ, but I did so merely in deference to the opinions of systematic workers, Messrs. Wilson and Evans and Rothschild, and more particularly to those of Dr. Gadow, who had availed himself of the opportunity of carefully studying the different forms side by side, whereas at that time I had secured no such facilities. Personally I was convinced that all belonged to one family—whether called Drepanididæ, Fringillidæ, or otherwise,—and always maintained this in my correspondence against general opposition, and that too at a time when Mr. Rothschild himself was setting forth descriptions of the Drepanines under such diverse families as Fringillidæ and Meliphagidæ! Although biological considerations first suggested to me the common origin of all the present family—honey-suckers and

thick-billed birds alike—yet at a very early period\* of my study of these birds I had excellent reasons apart from such for my belief. Before the body of the first *Pseudonestor* obtained by me was cold I was well aware that its tongue was essentially Drepanine and little modified, and that it indicated a positive connecting-link between the thick- and thin-billed sections, being, in fact, more typically Drepanine than that of the otherwise normal *Oreomyza*. The tongue of *Psittacirostra* likewise was taken from the bird immediately it fell to show that it was truly Drepanine, although much modified. In a hot country such parts should always be preserved immediately, as after a day's collecting they are liable to dry up and their appearance to become changed. The characters afforded by the nostrils and their opercula in all the important forms, as well as the pattern of colour, had been under my consideration as early as 1894, and it is doubtful whether any other important characters have been advanced since that time.

It is still my belief that the biological reasons on the strength of which I first concluded that all these birds belonged to one family are of the utmost importance, chief amongst which is the peculiar odour to be noticed in both groups, in the thin-billed and thick-billed forms alike. So far as Hawaiian birds are concerned, this odour is *absolutely restricted* to the Drepanines. Mr. Rothschild in his work on Laysan makes the astonishing statement that the Meliphagine Moho has a similar and even more powerful odour; but this is only one of those errors which, for want of due care, the museum naturalist is liable to make in opposing facts ascertained and proven in the field. The explanation is very simple: the Moho (*Acrulocercus*) *freshly*

\* It should be mentioned that a long time previously Dr. Selater (*cf.* Ibis, 1871, p. 559) had, after a careful study of various Hawaiian forms, expressly declared his opinion that two of the Finch-billed genera (*Psittacirostra* and *Lovioides*) were true Drepanines and related to *Heterorhynchus*—an opinion without doubt correct, since *Pseudonestor* is the connecting-link. It was not until long after I had come to the conclusion that not only these but also the most thick-billed genera were decidedly Drepanine, that Dr. Selater's views became known to me.

*killed or alive* \* has no such odour. The specimens supposed to possess it had no doubt been enclosed in boxes with Drepanines, or when collected in the field had been placed in a bag with them, and had thus become impregnated with their odour.

This odour, as I have pointed out in my former notes, cannot be acquired from the food, because it is found in forms of such diverse habits—*e. g.*, in *Drepanorhamphus* at times when it is feeding solely on the nectar of flowers, in weevil-eating *Heterorhynchus*, in *Psittacirostra* when it is devouring the red fruit of *Freycinetia*, in *Chloridops* when the sole contents of the crop are the seeds of the bastard sandal. Neither the Meliphagine birds nor the Flycatchers, when feeding in the same trees and on the same food as Drepanines, possess any such smell. All these facts point to the odour as being an ancestral character in the Drepanididæ.

In this connexion it may further be remarked that the song of the thick-billed *Pseudonestor* is practically identical with that of the various species of *Heterorhynchus*, which have always been allowed to be Drepanines, and that *Telespiza*, living isolated on the island of Laysan hundreds of miles distant from its allies, has a song similar to both. I shall not easily forget my astonishment when I first heard it on passing a house in Honolulu, and found on enquiry, not the expected *Heterorhynchus*, but *Telespiza*! Possibly the latter may have other notes, but the fact remains that the song I heard was note for note the same as that of the former species, and I heard it repeatedly.

#### 7. Cause of Frugivorous Habits in the Thick-billed Drepanididæ.

The thick-billed frugivorous Drepanids, like the purely or almost purely insectivorous members of the family, have no doubt assumed the habit for the same reason as the latter, *viz.* the competition for food, rendered unusually keen from the exceptionally small area of distribution. The development of the beak and the loss of the elaborate sucking-tongue have

\* The writer has on more than one occasion had *A. nobilis* alive.

naturally followed. In this connexion it is interesting to note that the rather strong-billed *Chlorodrepanis stejnegeri* of Kauai, so far as I know, stands alone amongst the brush-tongued forms in feeding freely on fruits; for at certain seasons it voraciously devours the berries of the poisonous *Wikstrœmia*, in the same manner as *Phœornis*. Such a species—becoming more and more frugivorous and abandoning flowers for fruits—may be considered as potentially the ancestor of a new series of thick-billed forms; at present it is largely a honey-sucker, largely insectivorous, and on occasion largely frugivorous. A line may be traced among the thick-billed forms of Hawaii through the purely insectivorous *Pseudonestor* to the largely frugivorous, but still largely insectivorous, *Psittacirostra*, ending in *Chloridops*, which has become almost entirely frugivorous.

#### 8. Distribution of Genera in the Islands.

The distribution of the genera within the group is very unequal, only five of the eighteen having a range which covers all the islands that are forest-clad. These are *Vestiaria*, *Himatione*, *Chlorodrepanis*, *Oreomyza*, and *Psittacirostra*. Three others, *Hemignathus*, *Heterorhynchus*, and *Loxops*, are found on four islands, a species of each inhabiting Kauai and a second Hawaii, the two extreme forest-bearing islands of the Archipelago. One, *Palmeria*, inhabits only Maui and the neighbouring island of Molokai. *Drepanorhynchus* is peculiar to Molokai, *Pseudonestor* to Maui, *Telespiza* to distant Laysan. Hawaii has no less than six genera peculiar to itself—*Drepanis*, *Ciridops*, *Viridonia*, *Loxioides*, *Rhodacanthis*, and *Chloridops*.

#### 9. Distribution of Species.

The distribution of the species is fully given in the table (p. 574). One form, *Heterorhynchus lucidus*, is almost certainly extinct, while several others, if not extinct, are so extremely rare as to be very nearly so. On examining the table of distribution it is at once noticeable that the birds may be divided into two very strongly contrasted classes.

Table of the Distribution of the Species of the Drepanidæ.

	HAWAII.	MAUI.	MOLOKAI.	LANAI.	OAHU.	KAUAI.	LAYSAN.
<i>Drepanis</i> .....	<i>pacifica</i> .						
<i>Drepanorhynchus</i> ..	.....	.....	<i>fuereus</i> .				
<i>Vestiaria</i> .....	<i>coccinea</i> .	<i>coccinea</i> .	<i>coccinea</i> .	<i>coccinea</i> .	<i>coccinea</i> .	<i>coccinea</i> .	
<i>Palmeria</i> .....	.....	<i>doli</i> .	<i>doli</i> .				
<i>Himatione</i> .....	<i>sanguinea</i> .	<i>sanguinea</i> .	<i>sanguinea</i> .	<i>sanguinea</i> .	<i>sanguinea</i> .	<i>sanguinea</i> .	<i>freethi</i> .
<i>Circidops</i> .....	<i>anna</i> .						
<i>Hemiphanes</i> .....	<i>obscurus</i> .	.....	.....	<i>lanaiensis</i> .	<i>elisiannus</i> .	<i>procerus</i> .	
<i>Heterorhynchus</i> .....	<i>wilsoni</i> .	<i>affinis</i> .	.....	.....	<i>lucidus</i> .	<i>hanapepe</i> .	
<i>Pseudonestor</i> .....	.....	<i>acanthophrys</i> .					
<i>Tiridonia</i> .....	<i>sagittirostris</i> .						
<i>Chlorodrepanis</i> .....	<i>virens</i> .	<i>virens</i> , var.	<i>virens</i> , var.	<i>virens</i> , var.	<i>virens</i> , var.	{ <i>parva</i> and <i>stepneyeri</i> .	
<i>Loxops</i> .....	<i>coccinea</i> .	<i>ochracea</i> .	.....	.....	<i>rufa</i> .	<i>ceruleirostris</i> .	
<i>Oreomyza</i> .....	<i>mana</i> .	<i>newtoni</i> .	<i>flammea</i> .	<i>montana</i> .	<i>maculata</i> .	<i>bairdi</i> .	
<i>Psittacirostra</i> .....	<i>psittacea</i> .	<i>psittacea</i> .	<i>psittacea</i> .	<i>psittacea</i> .	<i>psittacea</i> .	<i>psittacea</i> .	
<i>Loxioides</i> .....	<i>bailevi</i> .						
<i>Telespiza</i> .....	.....	.....	.....	.....	.....	.....	<i>cantans</i> .
<i>Rhodacanthus</i> .....	{ <i>palmeri</i> and <i>flaviceps</i> .						
<i>Chloridops</i> .....	<i>kona</i> .						

Thus *Oreomyza* is represented by a distinct species on each of six islands, as are also *Hemignathus*, *Heterorhynchus*, and *Loxops* on each of four. On the other hand, *Himatione*, *Vestiaria*, and *Psittacirostra* range over the whole main group, each with a single unmodified species. *Chlorodrepanis* occupies an intermediate position with two very distinct forms on Kauai, and another form, sometimes considered divisible into three or more species, ranging over the remaining islands. Of these, however, the distinguishing characters are so slight that it is questionable whether they are worthy even of subspecific rank, and in any case such characters are by no means to be considered equivalent to those which separate the different species of *Oreomyza*. The latter are clearly the results of isolation, one island having been colonized by a species from another, which has subsequently acquired peculiar characters. It might be supposed that the birds in the other class which shew no change on the various islands are in some way less susceptible to the effects of isolation. Probably this is not the case, and the true explanation is to be found in considering the habits of the members of the different genera.

*Himatione*, *Vestiaria*, and *Psittacirostra* are all birds which take extensive flights, often at a great height in the air, and frequently form small companies in these flights. If we stand on the main ridge of some of the islands the birds may be seen passing high overhead from leeward to windward or *vice versâ*. All freely traverse open country, in passing from one feeding-ground to another. Consequently when storms arise they are extremely likely to be carried across the channels between the islands, and no doubt this often happens. The birds of the other class, such as *Hemignathus*, *Oreomyza*, *Heterorhynchus*, &c., do not take these extensive flights, but keep closely to the forest, very rarely—and most of them never—venturing into the open. Very seldom would they be likely to get blown across from one island to another. In short there is little doubt but that individuals of *Vestiaria* and its class are transferred from one island to another sufficiently often to prevent any true isolation, which

is not the case with the other class. Who can fail to believe that a *Loxops* or a *Hemignathus* would have prospered on Molokai had they ever reached that island? Although *Himatione* ranges unchanged over six islands, yet after, by some remote chance, reaching the very distant Laysan it has there developed into a distinct form; and the case of the two extreme forms of *Chlorodrepanis* on the rather distant island of Kauai is also greatly in favour of my hypothesis.

That any of the Drepanine birds cross even the narrowest channels between the islands *willingly* is not to be thought of. In times of storm they are often blown down to the lowlands, sometimes in considerable numbers, in which case they mostly fail to regain the forest and perish after a few days. The only birds that I have myself picked up dead (sometimes in numbers) on the coast after these storms are of the genera *Vestiaria*, *Himatione*, and *Psittacirostra*; in fact, the very forms which by their habits are most liable to be carried away by the wind. Further, it is well known that, after stormy weather, the two former sometimes reach the bare island of Niuhau, across the considerable channel which separates it from Kauai, but they cannot live there long on account of its unsuitable nature. No doubt the majority of these unwilling emigrants perish, but it is certain that those blown from a high elevation on one island must not infrequently land in suitable forest-country on one of the others.

#### 10. *Richness of the Island of Hawaii in peculiar Forms.*

The relative richness in birds of Hawaii, with its eleven peculiar species and no less than six peculiar genera, is manifest and interesting, since in other groups of animals with highly peculiar species it is frequently (though not invariably) extremely poor, as compared with the older islands of the group. Probably its large area and very varying climate has favoured the multiplication of peculiar forms, while it must not be forgotten that, owing to its position at the end of the group of islands, it is incapable of sending forth emigrants except in one direction. That this

is of importance is rendered more likely from a consideration of the Drepanines of Kauai, at the other end of the group of forest-clad islands. Kauai, it is true, has no peculiar generic forms, although geologically so much more ancient than the large island; but being the most distant of the group, as well as at one extremity of the series of islands, its two species of *Chlorodrepanis* are by far the most isolated, its *Hemignathus* and *Loxops* are similarly circumstanced, while in the Meliphagines its Moho is very different to the other forms, which are closely allied *inter se*, and in the Turdidæ it has the two extreme forms of *Phæornis*. No doubt its small area and comparatively constant climate tend to render it much less rich in Drepanines than Hawaii.

#### 11. *Extreme Specialization of many Forms of Drepanine Birds.*

If, as is natural, we consider the primitive form of Drepanid to have been structurally very similar to such birds as are now comprised in the genera *Himatione* and *Chlorodrepanis*, and side by side with these place such forms as *Loxops*, *Drepanorhampus*, *Heterorhynchus*, and *Chloridops*, the remarkable specialization of the latter is at once apparent, though we are still able to examine connecting forms. To me this specialization indicates the severe competition that has taken place between the Drepanines in past ages. When a vast portion of the food-supply was derived from the blossoms of flowers, and this source of food, as I have shown, was relatively small to what it became later, change to a purely insectivorous, or largely frugivorous, diet must have been very advantageous to the individuals concerned, and the greater the specialization which resulted in obtaining some particular food (provided that it was sufficiently abundant), the greater the advantage to the species. To the field-naturalist who has examined many specimens of such a form as *Pseudonestor* at various seasons and found that its food consists essentially of the larvæ of a group of longicorn beetles peculiarly Hawaiian, and not less remarkable than the Drepanids themselves; who has seen how



perfectly modified it is for obtaining these; how perfectly adapted is the bill of such a form as *Drepanorhamphus* for obtaining the nectar from the deep tubes of the giant-blossomed Lobeliaceæ, inaccessible to other birds; how wonderful is the form of *Heterorhynchus*, which delights in the hard boring weevils, themselves equally noticeable; how powerful are the muscles of the head and beak of *Chloridops*, which can crack the stones of the ripe fruit of the bastard sandal; the extraordinary advantage of this specialization in each form for acquiring a constant supply of food almost or quite inaccessible to its allies, and that too in a country where the small land-area may be supposed to have rendered competition unusually keen, must appeal with the greatest force.

12. *High Specialization may become a Source of great Danger.*

This high degree of specialization, although of the greatest benefit under stable conditions, with a change of these obviously becomes a source of great danger. Thus, destroy the special food-supply of the birds mentioned above, and there is little doubt but that most of them would very quickly become extinct; for forms so perfectly adapted for special ends are, under ordinary circumstances, but ill-adapted to change their mode of life; and it is amongst such forms that most of the rarest species are found, while a considerable number of them already verge on extinction. It is probable that this state of things has largely been brought about by man, and in particular by the destruction of the lowest forest. Even now, in winter storms, large numbers of birds resort to the lowest skirts of the existing forest, generally at an elevation of 1200–1500 feet; and it is well known that in Cook's time such forms as *Psittacirostra*, *Himatione*, and *Chlorodrepanis* actually came down to the coast in Kealakeakua Bay, though now such flights would mean death to the visitants. Moreover, at these lower altitudes the flowering-season of most plants is different from that in the uplands, and they must have been an important source of food at seasons when it was scarce elsewhere.

13. *Other Causes of Extinction of Hawaiian Birds.*

Although the destruction of the lowest belt of forest over by far the greater part of the islands has, in my opinion, been a most efficient cause of the destruction of native birds, many other causes have been at work, all of which are due to the occupation of the islands by white men. Such causes are the introduction of cattle and goats, which have extirpated or very much thinned out great portions of the native forest; of cats, foreign rats, and the mongoose (which are direct enemies), as well as of the Mynah, which not only attacks and drives away other birds, but also devours their eggs and young. The disturbance caused by the entrance of cattle into untrodden forest appears to be alone sufficient to scare away some species. Thus, on a very rough lava-flow on Hawaii in 1892, the "Oo" (*Acrulocercus nobilis*) was very numerous, and as many as a dozen of these birds could be seen in a single tree, making, with hosts of the scarlet "Iiwi," the crimson "Apapane," and other birds, a picture never to be forgotten. A few years afterwards, on revisiting the spot at the same season, although the trees were, as before, one mass of flowers, hardly a single "Oo" was to be seen. The only noticeable change was that cattle were wandering over the flow and beginning to destroy the underbrush, just as they had already reduced the formerly dense forest bordering the flow to the condition of open park-land.

Cats were introduced into the Hawaiian Islands at a very early time, and, no doubt, increased excessively, while, as their owners moved from place to place, many strayed into the woods and began to feed on mice, rats, and birds. They are now found wild on all the islands, apparently only the wettest portions of the forest being free from them. On Lanai, in walking up a single ravine, I counted the remains of no less than twenty-two native birds killed by cats, and these must all have been destroyed within two days, as previously the whole gulch had been washed out by a heavy flood. Two cats were actually shot on this occasion as they were devouring their prey, and several others seen, but, owing to the fact that they are extremely shy and mostly nocturnal

in habits, few people who have not lived much in the woods have any idea of their numbers. The common rat is also quite at home in the forests and is decidedly arboreal in habits, feeding on fruits, land-molluscs, and no doubt on birds. The Mynah, which I have myself seen devouring both young and eggs of other species, has increased prodigiously, and probably exceeds in numbers the whole of the native land-birds put together. It has greatly extended its range through the forest since 1892, and on some of the islands is now ubiquitous.

#### 14. *Songs of Drepanine Birds.*

None of the Drepanids can be considered first-class songsters. The "Ou" (*Psittacirostra*) and the "Palila" (*Loxioides*) are, when at their best, distinctly pleasing, and surpass all the others. The "Akialoas," especially *Heterorhynchus*, have a song full of vigour, yet not beautiful nor sustained, but always delightful to hear, as being an expression of the highest contentment. This energetic outpouring of melody is noticeable likewise in *Pseudonestor*, *Hemignathus*, and *Chlorodrepanis*, the songs of all of which, as also those of *Loxops* and *Oreomyza* (when it does sing), bear a general similarity to one another. *Pseudonestor* and *Heterorhynchus* have an identical song; that of *Viridonia* is the same as that of *Chlorodrepanis*, with two or three notes added at the end. *Rhodacanthis* whistles several notes, which to anyone walking through the woods might appear to be rather the utterance of a man than of a bird. The songs of the other group of Drepanids are quite different. That of the "Iiwi" (*Vestiaria*) is harsh in the extreme. The song of the "Apapane" is short, monotonous, and often repeated, but not unpleasing. It has a singularly plaintive call-note. The "Mamo" (*Drepanis*) and the allied form on Molokai have an identical cry, except that in the latter at its best it is probably much louder. The song of *Palmeria* is peculiar, as it makes a remarkable vibrating or gurgling sound. In spite of the dissimilarity in the normal songs or cries of the birds of this section, most of the different forms frequently utter calls or notes very similar to one another. They are more varied than

the almost universal squeak of the call or alarm-note of the green-feathered section.

The subjoined list will enable anyone to distinguish at a glance the various genera of Drepanididæ. More characters are frequently given there than are necessary for merely separating the different forms, especially where these characters appear to me to be of great importance. It is only necessary to add that the views expressed in this paper on the Drepanine birds have not been formed off-hand, but are the results of much study and observation, extending over a period of ten years, six of which have been spent in the islands themselves, for the most part in the haunts of the various species. As the writer has had the opportunity of seeing many of the rarest forms—not a few individuals only, but scores or hundreds—he has had ample opportunity for careful study of the habits, without the need or desire to kill a valuable specimen whenever seen. For this reason the biological considerations may be held to be of more importance than would be the case were they based on a mere superficial study extending over a short period of field-work.

*Table of Genera of Drepanididæ.*

- 1 (2). Apices of some of the primaries truncate, *or* if not truncate, then the front of the head bearing a large crest of narrow curved feathers, which overhangs the base of the beak.  
 Plumage of upper parts always partly black, the rectrices always black (sometimes white-tipped), the wings always at least largely so.  
 White markings always present in the adult, either on the wings or upper parts of the body, at times confined to the outer web of some of the primaries.  
 Young birds with body-feathers always of a black or dark obscure colour, either wholly or in part; when with many pale feathers (*Vestiaria*), then these are spotted with black . . . DIVISION I.
- 2 (1). Apices of primaries never truncate; head never with a crest of narrow curved feathers.  
 Plumage of adults never in the least black above, not even the tail black.  
 Young birds never clothed with black or dark obscure plumage, nor black-spotted, but always largely green or olivaceous.

DIVISION II.

## DIVISION I.

- 1 (6). Beak very long and strongly curved, as long as or longer than the metatarsus.
- 2 (5). Beak black, wholly or in great part; plumage mainly black or black and yellow. Feathers of throat not modified.
- 3 (4). Plumage black and yellow; nasal opercula not very long . . . . . *Drepanis*.
- 4 (3). Plumage not at all yellow; nasal opercula very much elongated . . . . . *Drepanorhamphus*.
- 5 (2). Beak entirely pale; plumage of adult scarlet, of young yellowish and black-spotted; feathers of throat much modified, narrow, and stiff . . . . . *Vestiaria*.
- 6 (1). Beak never very long, straight or but little curved.
- 7 (8). A large crest of pale feathers curving over the base of the beak . . . . . *Palmeria*.
- 8 (7). Head without a crest.
- 9 (10). Beak moderately long, sharply pointed; body-plumage not variegated with strongly contrasted colours . . . . . *Himatione*.
- 10 (9). Beak rather Finch-like; body-plumage highly variegated . . . . . *Ciridops*.

## DIVISION II.

- 1 (4). Beak extremely long and one or both of the mandibles strongly curved, the upper one always so and very slender and delicate at its apical portion—so slender as often to be even slightly flexible.
- 2 (3). Upper mandible only a little longer than the lower, nasal setæ altogether wanting . . . *Hemignathus*.
- 3 (2). Upper mandible greatly exceeding the lower (by from  $\frac{1}{2}$  to  $\frac{1}{3}$  its own length), nasal setæ well developed . . . . . *Heterorhynchus*.
- 4 (1). Beak not of extraordinary length and much curved; if moderately long and curved, then the apical portion of the upper mandible not extremely slender and very little longer than the lower.
- 5 (14). Beak never of very robust form, like that of a Grosbeak, nor of heavy build, with the upper mandible conspicuously surpassing

the lower; if (as in *Loxops*) the beak is short and like that of a small Finch, then the lower mandible is more or less distorted either to the right or left, the tail is elongated and conspicuously forked, and the birds themselves are of very small size.

- 6 (13). Tail more or less short, not long and distinctly forked; lower mandible not deflected; beak not short and robust, like that of a small Finch.
- 7 (8). Beak straight, long, and strong, about as long as the metatarsus. (No well-marked sexual distinctions in plumage of adults. Tongue long, brush-like, typically Drepanine.) ..... *Viridonia*.
- 8 (7). Beak curved or straight, if straight then much shorter than in 6.
- 9 (10). Beak more or less curved, generally distinctly so; nasal setæ always present and well developed. Tongue typically Drepanine, long, and brush-like. (Well-marked sexual distinctions in plumage of adult, the male much brighter in colour.) ..... *Chlorodrepanis*.
- 10 (9). Beak straight or not curved as in 9; distinct nasal setæ or setiform feathers may be present or entirely wanting. Tongue abnormal, flattish, slightly cleft at the apex, not of the typical tubular brush-like form.
- 11 (12). Nasal setæ or modified setiform feathers well developed, so as to be able to shield the whole length of the nasal-openings. (Colour of sexes little differentiated.) .. *Oreomyza*.
- 12 (11). Nasal setæ or setiform feathers entirely absent, or at least very short and little developed, not able to shield the nasal openings. (*Sexual coloration of adults markedly different.*) ..... *Pavoreomyza* \*, subgen. nov. :  
type *Oreomyza maculata*.
- 13 (6). Tail elongated, distinctly forked at apex; lower mandible more or less deflected; beak short, but stout, like that of a small Finch. (Tongue typically Drepanine.) .. *Loxops*.

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\* Herein I place also the other three species with sexual dimorphism.

- 14 (5). Beak always strong, often excessively powerful and heavy, sometimes with the upper mandible conspicuously surpassing the lower. Robust birds, never very small.
- 15 (18). Beak with the upper mandible greatly or very greatly surpassing the lower in length, never very broad towards the base in dorsal aspect, more or less and sometimes very strongly compressed laterally. Body above with green plumage.
- 16 (17). Upper mandible very strongly flattened, or compressed laterally and high. Tail very short, as in *Heterorhynchus*. Coloration of adults nearly similar in both sexes, each with only a yellow superciliary line on head. (Tongue not typically Drepanine, but more so than that of *Oreomyza*, rather elongated.) . . . . . *Pseudonestor*.
- 17 (16). Upper mandible not very strongly compressed laterally, subcariniform. Tail not extremely short. Colour of adults dissimilar in the two sexes, the male with crown of head bright yellow. (Tongue degraded from the typical honey-sucking organ, but Drepanine characters still distinguishable.) . . . . . *Psittacirostra*.
- 18 (15). Beak with upper mandible only slightly (though distinctly) surpassing the lower in length and more swollen laterally, often very much so, so that in most forms the nasal openings appear to be quite dorsally placed and the beak very broadly rounded above. Colour of plumage of body above not always green.
- 19 (20). Beak strong, but not excessively powerful and heavy, much less so than in the following. Plumage of body above ashy grey in adults. Colour of sexes a little different, the yellow of the head in female less bright . . . . . *Lovioides*.
- 20 (19). Beak excessively heavy and powerful. Plumage of body above not ashy grey.
- 21 (24). Upper mandible in dorsal aspect of very elongate triangular form. Upper and lower mandibles well adapted to one

another. Male at least with the plumage of the head contrasting in colour with that of the upper parts of the body.

- 22 (23). Beak with cutting-edge of lower mandible distinctly and evenly curved on the apical part. Immature birds without dark spots above. (Very great differences in colour between the sexes when adult, the female remaining much like the young of either sex.) ..... *Rhodacanthis.*
- 23 (22). Beak with cutting-edge of lower mandible not distinctly and evenly curved. Immature birds with dark spots ..... *Telespiza.*
- 24 (21). Upper mandible in dorsal aspect with the sides not very strongly convergent to the apex, so as to form a very elongate triangle. Cutting-edges of mandibles irregular, so that they are not perfectly adapted to one another. Plumage of head in neither sex conspicuously different to that of the body above. (No marked difference in colour of sexes.) .. *Chloridops.*

The list of genera given above calls for a few remarks. In the first division the position of the abnormal *Ciridops* appears to me quite certain. Its characteristic black wings and tail, and the presence of white (not quite clear white) feathers, its scarlet plumage, to my mind so extremely like that of *Vestiaria*, and the blackish-grey feathers of the throat, so similar to what may be seen in *Palmeria*, leave no question as to its affinities. In the second division the ashy plumage of *Loxioides* appears aberrant at first sight, but it is noteworthy that others of the "green" section pass through a phase of plumage very similar to this (*e. g.*, certain species of *Loxops* &c.), which shews how easily it may have been acquired. *Telespiza* in the dark-spotted plumage of the young is also aberrant, but this condition does not appear to me comparable with the dark or black-spotted plumage of the first division. Its position in the second or green section is obvious, and *Rhodacanthis* might well be united with it generically.